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Expanding Geographical and Ecological Range of *Platynota stultana* in California (Lepidoptera: Tortricidae)

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The moth that later became known to American economic entomologists as the "omnivorous leaf-roller," *Platynota stultana* (Walsingham), was described from specimens collected by H. K. Morrison in the "Province of Sonora," Mexico (Walsingham, 1884). Probably the locality was near the international border because Morrison's biographers state that he worked in Arizona during 1881 and New Mexico in 1882 (Mann, 1885), or 1882 and 1883 in Arizona (Smith, 1885), but they do not mention Mexico among his expeditions. The species was collected in what is now Cochise County in southeastern Arizona in the 1890's by F. H. Snow (AMNH, CU, KU)[1] and in Sinaloa, Mexico, as early as 1893 (USNM), so the native range probably included semiarid parts of northwestern mainland Mexico and adjacent southwestern United States.

As the common name implies, a broad array of larval hostplants is known. Atkins *et al.* (1957) summarized records representing about 20 families of Angiospermae, most of which arose from urban and agricultural situations, whence the insect has expanded its geographical range during the past 80 years. *Platynota stultana* evidently was not native in cismontane southern California, because it was not encountered in the early years of citrus investigations, during the 1880's and 1890's, yet it became a conspicuous pest by 1913–1915 (Woglum, 1920).

History of Occurrence in California

Data associated with specimens examined (see acknowledgments) and in the files of the California State Department of Food and Agriculture indicate the following history of introduction and spread within the state.

The earliest records I have seen are in Los Angeles County, 1898 at La Mirada and 1904 at Los Angeles (USNM). Had the species been native in the vicinity of southern California towns, it certainly would have been encountered by Coquillett, who reared and collected many microlepidoptera during 1883–1892 in the Los Angeles area. As a comparison, there are a number of 1880's records for the orange tortrix, *Argyrotaenia citrana* (Fernald), a moth with similar larval and adult habits and life history (Powell, 1964). By 1913–1915, however, *P. stultana* had become an economic problem in several citrus and cut flower growing areas of Los Angeles and Orange counties (Woglum, 1920; Bohart, 1942). Other early collections of *P. stultana* include occurrences at San Diego, 1913 (SDNH), Needles on the Colorado River, 1918 (CU), and San Bernardino by 1925. The species also expanded southward, into Baja California, having been taken at Ensenada, in 1941 (USNM).

[1] See acknowledgments for list of institutional abbreviations.

Northward, *P. stultana* was taken at Saticoy, Ventura County, in 1925 (USNM), and it reached coastal Santa Barbara County by 1940, although the date of initial establishment and continuous residency there is unknown. There is a record for Carpinteria in 1940 (CDFA), and *P. stultana* was reared from larvae during the Channel Islands Biological Survey, on Anacapa Island, the same year (LACM). The species evidently did not continue its northward expansion along the coast, as there are no records north of Santa Barbara in field situations during the subsequent 20 years.

Once established in southern California, a diversity of ornamental and agricultural plants was adopted. Records include tomato (*Lysopersicon*) (1898); *Portulaca* (1904); *Citrus* and carnation (*Dianthus*) (1913); avocado (*Persea*) and walnut husks (*Juglans*) (1925); pepper pods (*Capsicum*) (1926); pigweed (*Chenopodium*) and *Malva* (1929); youngberries (*Rubus*) (1932); sugar beet (*Beta*) and *Cyclamen* (1934) (USNM records). There were many interceptions of larvae in bell peppers from Sinaloa at Nogales and Los Angeles during the late 1920's and 1930's, resulting in a federal quarantine (Busck, 1933).

By contrast, there are few records of *P. stultana* on native plants. Goeden and Ricker (1976a,b) encountered the species on native ragweeds (*Ambrosia*) in desert areas and in roadside, abandoned cropland, and other artificial expansions of *Ambrosia* habitat in cismontane southern California. Also in the 1970's, the species was reared by Gorelick from *Eriogonum grande* Greene, an insular endemic plant, on Santa Catalina Island (CIS).

There are specimens from Sacramento reared in 1932 from alfalfa, and in nursery situations during 1943–1945 (CDFA), but it appears that populations have not been established continuously in the Sacramento Valley, because there are no records for field situations between 1932 and 1955. Similarly, the omnivorous leaf-roller was recorded in greenhouses in the San Francisco Bay area in 1940–1941 (Bohart, 1942); at Salinas, Monterey County, in 1955 (CDFA); and in Alameda County at San Leandro (1957) (CDFA). However, prior to 1955, there are no confirmed records of *P. stultana* established in the field anywhere north of the Transverse Range, which separates cismontane southern California from the rest of the state.

In the late 1950's and during the following several years, populations of this insect greatly expanded their geographic and ecological ranges in California. The data suggest that changes in physiological tolerance developed in relation to physical factors.

In 1956 adults of *P. stultana* were taken at lights in urban Davis, Yolo County (20 km west of Sacramento) (CIS). Although I did not encounter the species during three months' sampling in Kern County in 1955, it appeared in agricultural field situations there in 1959, in a light trap at Bakersfield in July (CIS), and feeding on cotton flowers and fruit at Edison (10 km ESE of Bakersfield) in August (CDFA). The following year *P. stultana* was taken on cotton at McFarland (40 km NNW of Bakersfield), and during 1961–1963, the omnivorous leaf-roller quickly spread throughout the San Joaquin and southern Sacramento valleys (Map 1). It acquired considerable notoriety as a new pest of vineyards, beginning in 1963 (Lynn, 1969; Ali Niazee and Stafford, 1972).

Platynota stultana reached the Monterey Bay area and inner Contra Costa County (Antioch) by 1967 and Glenn County in the northern Sacramento Valley by 1968 (CIS, CDFA). Although there had been sporadic nursery and greenhouse records in the San Francisco Bay area for more than 25 years, *P. stultana* was not recorded out of doors until 1967, when it was reared from potted *Senecio* at Albany, Alameda County (Frick and Hawkes, 1970; CIS). Adults first appeared at lights in 1979, when they were collected in Berkeley (CIS). Its late establishment on Santa Cruz Island, in the mid 1970's (Powell, 1981) is postulated to be the result of introduction by man following broader ecological adaptation by populations of adjacent mainland areas, where *P. stultana* apparently was localized and was rarely encountered during the 1940's and 1950's.

Increased Diversity of Larval Hostplants

In the process of the 1960's expansion, *P. stultana* adapted to a wider diversity of plants, including conifers and both dicotyledons and monocotyledons, a much greater taxonomic array featuring more diverse chemical and physical characteristics, than the herbaceous angiosperms adopted in southern California during the early part of the century. Thus, the physiological tolerance by *P. stultana* expanded to encompass gymnosperms, including Pinaceae (*Pinus*) (Yolo Co., 1966), Cupressaceae (*Juniperus*) (Fresno Co., 1966), and Taxaceae (*Taxus*) (Monterey Co., 1967); monocotyledons, Poaceae, including *Zea* (Tulare Co., 1963 and Kern Co., 1969), *Sorghum* seed (Glenn Co., 1969); various additional legumes, including *Phaseolus* (Stanislaus Co., 1961), *Albizia* (Kings Co., 1964), and *Arachis* (Fresno Co., 1966); as well as Vitaceae and exotic representatives of many plant families, such as Begoniaceae, Celastraceae, Aquifoliaceae, Theaceae, Aizoaceae, Ginkgoaceae, and Ebenaceae (CDFA records), additional to host records summarized by Atkins *et al.* (1957).

Conifers, monocotyledons and legumes are kinds of plants generally used by microlepidoptera that are specialized in terms of larval foods (Powell, 1980), and none of these hosts had been recorded as a foodplant of *P. stultana* in California prior to 1950. There is some indication that expanded host selection has taken place in southern California populations as well, for example use of *Ginkgo* (1961), *Juniperus* (1970), and *Trifolium* (1971) in Santa Barbara County (CDFA).

Whether physiological tolerance to physical factors such as high rainfall, low temperature winters also broadened is problematic. There are early records for desert areas, e.g., Needles (1918); Yuma (1925, 1928); and in San Diego County at San Felipe Wash (1935) and Borrego (1941) (AMNH, USNM), indicating that survival in arid climatic situations of extreme temperature ranges occurred. Nonetheless, range expansion of field populations into northern California seemed to take place contemporaneously with broader hostplant use.

Discussion

Inconsistencies of sampling notwithstanding, it seems apparent that after colonization around the turn of the century, *Platynota stultana* became widely established and adapted in southern California during the following 20 years, remained stable for another 30 years, then expanded its range in a relatively short time to encompass low elevation areas in most of the rest of the state. The maximum area (greatest right-angle, straight line distances) occupied in California during 1915–1950, some 80,000 square km, more than tripled, to ca. 270,000 square km, during 1956–1968, with an increase in latitudinal range from 1°45′

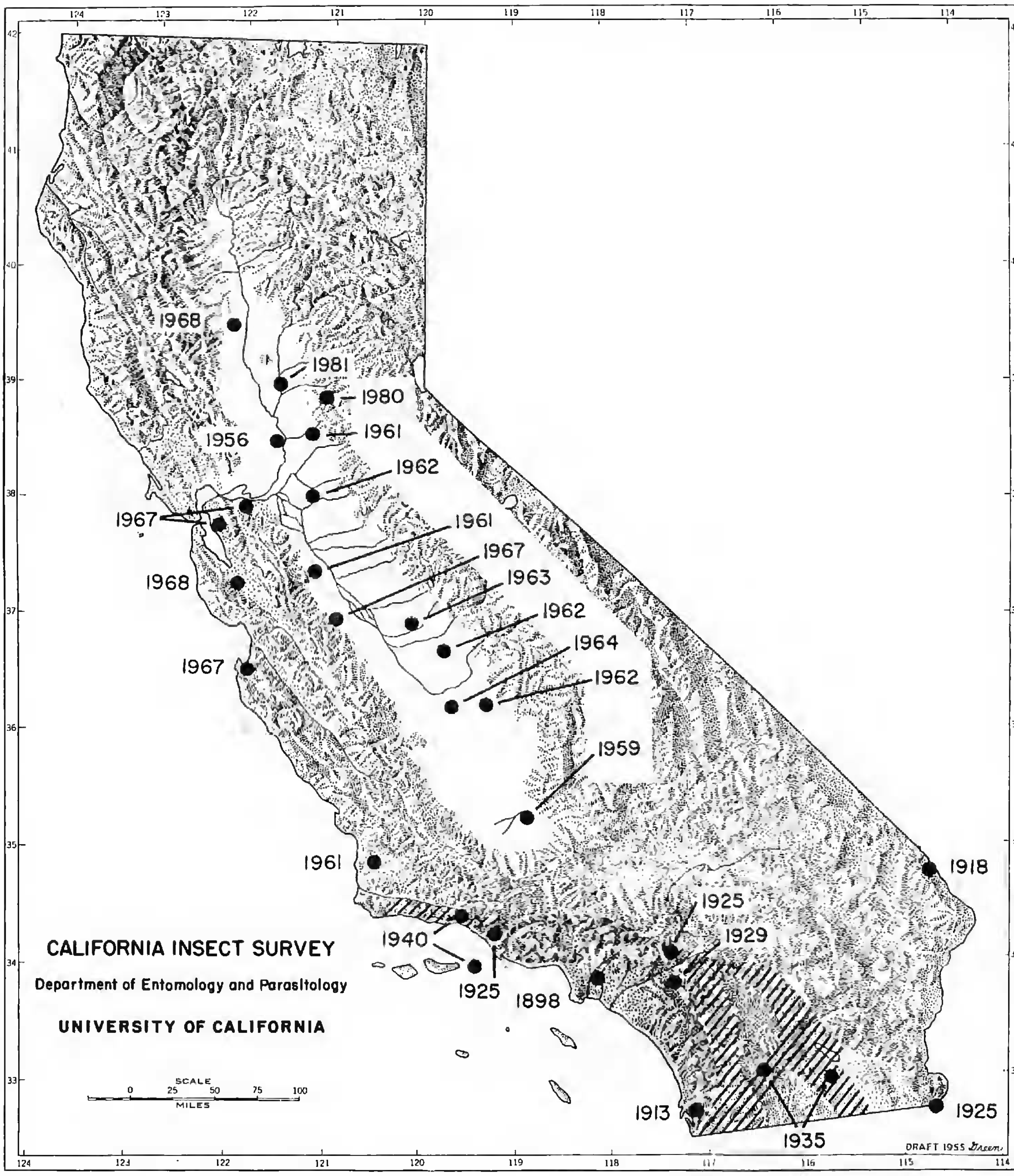

Fig. 1. Geographical distribution of *Platynota stultana* in California: by 1925 (dark shading); additional areas known to be inhabited by 1940 (cross hatched); later dated localities refer to first records in counties north of the Transverse Ranges.

to 6°45′ (Fig. 1). At the same time there was adaptation to a considerably greater spectrum of environmental conditions, particularly larval foods, shorter frost-free season, and increased total precipitation.

A similar kind of range expansion, establishment followed by gradual encroachment in a restricted area for a long time, then rapid enlargement of the area occupied, has been observed for other introduced insects. For example, the European skipper butterfly, *Thymelicus lineola* (Ochsenheimer), was discovered in southern Ontario in 1910. Its early progress is poorly documented, but because butterflies are the best surveyed group of insects and because this species is a pest of Timothy grass, the progress of its distribution in later years could be reconstructed with reasonable confidence (Burns, 1966). From 1910 to 1950 the range did not enlarge much, southwestward as far as Findlay in northern Ohio (1927) and the vicinity of Ann Arbor, Michigan (1949), and northeastward to Toronto (1945) and Niagara Falls (1948), a maximum range of ca. 46,000 square km. Suddenly, during 1953–1965, records from widely scattered areas appeared, indicating that populations had expanded in all directions, to encompass most of the northeastern U.S. and adjacent parts of Canada, from New Brunswick west to Lake Superior and south to Maryland, a maximum area of ca. 1.5 million square km. In addition, a colony was discovered in British Columbia, which may have resulted from an independent introduction from Eurasia or via railroad from the east (Burns, 1966).

It is probable that saltatorial range expansions following a period of slow progress by colonist species often are masked by inadequate documentation of the history of spread, or even that such bursts might appear to have occurred because of gaps in the record. Thus, the Old World earwig, *Euborellia annulipes* (Lucas) seems to have undergone a history in California similar to that of *Platynota stultana*; i.e., widespread establishment in southern California and at coastal stations northward, from 1880 (and probably much earlier) to the 1920's, then a rapid expansion during 1932–1941, in which the Central Valley, Coachella Valley, and Colorado River areas were occupied (Langston and Powell, 1975). By contrast, an apparent accelerated expansion of the European tortricid moth, *Croesia forskåleana* (L.) in the northeastern U.S., was interpreted to be an artifact of lack of effort by resident collectors (Powell and Burns, 1971). In both examples early collection records are sporadic, however, and precise details of the range extensions cannot be retraced.

The best documentation of insect introductions and subsequent spread have come from examples of classical biological control. DeBach (1965) summarized criteria of colonization and pointed out that only ca. 20–25% of attempted introductions have resulted in successful establishment and then complete preadaptation to the new environment usually seems to have been the rule. DeBach discussed two possible cases of latent increase in adaptive fitness in entomophagous insects. In one, *Comperiella bifasciata* Howard (Aphelinidae), large releases of progeny from a small founder colony (5 mated females) were made in various parts of southern California in 1942. By 1946 it was apparent that establishment was successful only at Riverside. During 1948–1957, however, the colonist populations spread westward and southward to inland districts of Los Angeles and San Diego counties and continued to increase in abundance during the next several years.

On theoretical evolutionary grounds, the most plausible explanation of delayed ecogeographical expansions by introduced insects is one of increased genetic fitness to environmental conditions in areas peripheral to the new home. It is generally believed that introductions often consist of few founders. When their genetic preadaptation sufficiently meets physical and biotic demands of the environment at the place of introduction, colonization may be successful, often with establishment aided by release from biotic population controls in source populations. This sets the stage for possible acceleration of evolutionary change. Selection pressure at the margins of expanding founder populations may promote increased physiological adaptedness to environmental situations to which the founders, or even the source populations, were not preadapted.

DeBach (1965) warned that observed long-term changes in distribution and abundance of introduced species may be due to ecological factors rather than genetic change. In particular, as demonstrated by population trends in several aphelinid parasitoids of scale insects in California, competitive displacement either by later arriving introduced species or by competitors already established, may comprise an important, though cryptic influence affecting changes in populations. Thus, for example, before assuming that increase in the distribution of *Thymelicus lineola* was due to genetic change, we should consider whether ecological factors, especially competition with native species of grass-eating Hesperiinae, might have been involved. It would be interesting to search for changes in relative abundance or distribution of native hesperiine species in the Great Lakes-Northeastern U.S. region since 1950, and in changes in host grass selection by *T. lineola.*

By contrast, competitive displacement seems less likely in phytophagous, holometabolous species that are polyphagous as larvae, or in general feeders and scavengers such as earwigs. Certainly it would be much more difficult to document than in examples of closely related, specific feeders occupying similar niches to one another. If altered genetic fitness is responsible for latent bursts of expansion, the numbers of generations required presumably would vary widely with differing selective regimes. On the average, for a univoltine insect such as *Thymelicus,* a considerably longer period might be expected (e.g., 40–50 years), than for a homodynamic species such as *Comperiella* or *Platynota* with several annual generations (e.g., 5–20 years).

Acknowledgments

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Dedication

This paper is dedicated to Prof. R. M. Bohart in commemoration of his long and remarkably productive career, which included early work with *Platynota stultana* and other California microlepidoptera. Twenty-nine years ago Bohart and I participated in the University of California summer field course in Entomology, his initiation as an instructor and mine as a student. No doubt he recovered from the experience in a few years, but I never did, for my attention had been irrevocably turned from large to small insects, the really "innersting" ones.

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